

LIVING WITH THE ENEMY: JUMPING SPIDERS THAT MIMIC WEAVER ANTS

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ABSTRACT. Ants prey on salticids, and encounters with weaver ants (*Oecophylla smaragdina* (Fabricius 1775)) appear to be especially dangerous for many salticids. In the Philippines, *Myrmarachne assimilis* Banks 1930 is a salticid that mimics *Oecophylla smaragdina*. We tested for the abilities of four categories of salticids, plus *M. assimilis*, to survive in the proximity of weaver ants. The four categories were: (1) myrmecomorphic (ant-like species other than *M. assimilis*); (2) myrmecophagic (ant-eating species); (3) myrmecophilic (a species that is either myrmecophagic nor myrmecophagic, but is known to associate with ants) and (4) ordinary (species that are neither ant-like nor ant-eating, and are not known to associate with ants). The hypothesis investigated here is that *M. assimilis* has, compared with other salticids, especially pronounced ability to survive in close proximity with this particular ant species. The individual salticids used in our experiments had not had previous contact with weaver ants or any other ants. When confined with groups of 10 weaver ants, the myrmecomorphic, myrmecophagic and myrmecophilic species survived significantly more often than ordinary salticids, but *Myrmarachne assimilis* survived significantly more often than all other categories. When kept with groups of 20 ants, there was a proportional decrease in the number of salticids that survived within each salticid category. However, few salticids survived when confined with groups of 40 ants, regardless of category.

Keywords: Salticidae, mimicry, predation, myrmecomorphy, myrmecophily

In the Philippines, *Diacamma rugosum* (Le Guillou 1842) (previously known as *D. vagans*), *Dolichoderus thoracicus* Stitz 1925 (previously known as *D. bituberculatus*), *Oecophylla smaragdina* (Fabricius 1775), *Odonotomachus* sp., *Polyrachis* spp. and *Solenopsis geminata* (Fabricius 1804) are ants that prey on jumping spiders (Salticidae) (Nelson et al. 2004). In an earlier laboratory study (Nelson et al. 2004), four categories of salticids were tested with these same ant species to measure their ability to survive in the presence of ants: (1) myrmecophagic species (i.e., species that select ants as preferred prey; see Li & Jackson 1996), (2) myrmecomorphic species (i.e., species that resemble ants; see Jackson & Willey 1994; Cushing 1997), (3) myrmecophilic species (i.e., a salticid species that is neither myrmecophagic nor myrmecomorphic, but known to associate with ants; see Nelson et al. 2004) and (4) ordinary species (i.e., species that are not known to associate with ants and are nei-

ther ant eaters nor ant mimics; see Jackson & Pollard 1996). These tests were carried out in small cages (diameter 90 mm) by putting one salticid together with one or with five ants per cage and then measuring how many spiders survived after 10 h with the ants. The ordinary salticids had the least success at surviving these tests, suggesting that ant eaters, ant mimics and ant associates have generalized adaptations that enhance their abilities to survive in the presence of a variety of ants, at least when the number of ants is small.

Here we investigate the ability of a variety of salticids to survive in the presence of numerous ants in large cages and we focus on a particular ant species, *Oecophylla smaragdina*. There are two species in the genus *Oecophylla*, *O. smaragdina* in tropical Asia and Australasia and *O. longinoda* (Latreille 1802) in tropical Africa. Known as 'weaver ants', these two species often dominate local arboreal habitats (Vanderplank 1960; Lokkers

1986) where they make nests by spinning leaves together with silk. The larvae of *Oecophylla* secrete the silk (Doflein 1905), but the workers determine where the silk goes. By carrying the larvae about and moving them across locations in need of silk, the major workers of *Oecophylla* use the larvae as nest-building tools (Hölldobler & Wilson 1977a). Minor workers generally remain inside the nests, whereas the more numerous major workers leave the nests and function as aggressive predators and soldiers for the colony (Hölldobler & Wilson 1977b, 1978; Hölldobler 1983). A single *Oecophylla* colony, with one queen, is typically spread across numerous nests and sometimes more than one tree (Hölldobler & Wilson 1977c). As many as half a million workers may live in a single colony (Hölldobler 1983).

Different species of *Myrmarachne* resemble different ant species (Wanless 1978; Edmunds 2000), but *Myrmarachne assimilis* is unique among the Philippine species studied because it alone resembles *O. smaragdina*. For *Myrmarachne*, myrmecomorphy appears to function primarily as Batesian mimicry, where predators that avoid the model (the ant) also avoid the mimic (the salticid). However, Batesian mimics of ants may be forced to 'walk a tightrope', needing to 'live with the enemy'. They need to be close to the model for safety from other predators but at the same time they need to avoid becoming the model's prey (see Reiskind 1970; Edmunds 1974; Elgar 1993; Oliveira 1988). Weaver ants appear to be exceptionally aggressive, yet *M. assimilis* routinely keeps close company with weaver-ant colonies in nature.

Cuticular hydrocarbons are used by many ants for distinguishing between nestmates and non-nestmates (Hölldobler & Wilson 1990; Thomas et al. 1999; Wagner et al. 2000). Chemical mimicry of ants has been reported for the salticid *Cosmophasis bitaeniata* (Keyserling 1882) (Allan & Elgar 2001; Allan et al. 2002; Elgar & Allan 2004). Perhaps in the field *M. assimilis* uses some form of chemical communication to avoid predation by *O. smaragdina*. However, the objective of the present study was not to investigate a hypothesis about mimics exploiting the nest-mate recognition system of *O. smaragdina*. Instead, our objective was to investigate whether *M. assimilis* might have evolved adaptations that

make it especially proficient at surviving in the presence of its model even in the absence of opportunity to acquire nest-mate cues. The salticids we used were from laboratory cultures and could not have acquired any host-specific cuticular hydrocarbons by feeding on ants or through direct contact with ants (see Elgar & Allan 2004) because the individuals we used had never encountered ants before being tested. We tested different types of salticids in the laboratory by confining them in cages with groups of weaver-ants, our prediction being that *M. assimilis* would survive often more than other salticids, including other myrmecomorphs that do not specifically mimic weaver ants.

METHODS

In the Philippines, our study site was the vicinity of Los Baños (Laguna Province, Luzon, 14°10' N 121°14' E), including a rain forest habitat at Mt. Makiling. Laboratory tests were performed at the International Rice Research Institute (IRRI) in Los Baños. When needed, we collected weaver ants from the field, but all salticids used in experiments came from laboratory cultures and none had prior experience with ants of any species. No individual salticid nor any individual ant group was tested more than once. Tests were aborted whenever two or more ants died during testing, but this rarely happened. For each salticid species, a series of tests was carried out using both mature females and juveniles. Body length of the adult salticids varied (see Nelson et al. 2004) and juveniles were used when they were 3mm long. Salticid maintenance procedures were the same as in earlier spider studies (Jackson & Hallas 1986).

All tests began at c. 0800 hours and lasted 10 h (laboratory photoperiod 12L:12D, lights on at 0700 hours) and consisted of placing a single salticid in a cage with either 10, 20 or 40 ants. At the end of each test, we counted how many salticids were still alive. Our objective in this study was only to compare the percent survival for the different groups of salticids. Latency to attack and the behavior of ants and spiders during the tests were not recorded. Survival data were analyzed using tests of independence (Sokal & Rohlf 1995), with Bonferroni adjustments being applied whenever multiple comparisons were made using the same data sets (see Rice 1989).

Table 1.—Salticids used in tests with ant workers in laboratory. Ordinary salticid: species that are not known to associate with ants and are neither ant eaters nor ant mimics. Myrmecophagic salticid: species that select ants as preferred prey. Myrmecomorphic salticid: species that resemble ants. Myrmecophilic salticid: a salticid species that is neither myrmecophagic nor myrmecomorphic, but known to associate with ants.

Species of Salticidae	Category
<i>Bavia sexpunctata</i> (Doleschall 1959)	Ordinary salticid
<i>Chalcotropis gulosa</i> (Simon 1902)	Myrmecophagic
<i>Chalcotropis luceroi</i> Barrion & Litsinger 1995	Myrmecophagic
<i>Cosmophasis estrellaensis</i> Barrion & Litsinger 1995	Ordinary salticid
<i>Epeus hawigalboboguttatus</i> Barrion & Litsinger 1995	Ordinary salticid
<i>Harmochirus brachiatus</i> (Thorell 1877)	Ordinary salticid
<i>Heratemita alboplagiata</i> (Simon 1899)	Ordinary salticid
<i>Lagnus</i> sp.	Ordinary salticid
<i>Mantisatta longicauda</i> Cutler & Wanless 1973	Ordinary salticid
<i>Menemerus bivittatus</i> (Dufour 1831)	Ordinary salticid
<i>Myrmarachne assimilis</i> Banks 1930	Myrmecomorphic
<i>Myrmarachne bakeri</i> Banks 1930	Myrmecomorphic
<i>Myrmarachne bellicosa</i> (G. & E. Peckham 1892)	Myrmecomorphic
<i>Myrmarachne bidentata</i> Banks 1930	Myrmecomorphic
<i>Myrmarachne maxillosa</i> (C. L. Koch 1846)	Myrmecomorphic
<i>Myrmarachne nigella</i> Simon 1901	Myrmecomorphic
<i>Orthrus bicolor</i> Simon 1900	Ordinary salticid
<i>Phintella piatensis</i> Barrion & Litsinger 1995	Myrmecophilic
<i>Portia labiata</i> (Thorell 1887)	Ordinary salticid
<i>Plexippus petersi</i> (Karsch 1878)	Ordinary salticid
<i>Siler semiglaucus</i> Simon (1901)	Myrmecophagic
<i>Telamonia masinloc</i> Barrion & Litsinger 1995r	Ordinary salticid
<i>Thiania</i> sp.	Ordinary salticid
<i>Xenocytaea</i> sp.	Myrmecophagic

We tested 24 salticid species (Table 1), all of which were also used in the earlier study (Nelson et al. 2004). Statistical analysis was based on the *a priori* categories from the earlier study, plus one additional *a priori* category (mimic of the weaver ant, *M. assimilis*). Other than *M. assimilis*, these categories were: myrmecomorphic salticids (*Myrmarachne* species other than *M. assimilis*); myrmecophagic salticids, ordinary salticids and a myrmecophilic salticid (Table 1). Voucher specimens of all species have been deposited in the IRRI Taxonomy Laboratory in Los Baños and in the Florida State Collection of Arthropods in Gainesville.

The testing apparatus was a cylindrical plastic cage (diameter & height c. 200 mm) with a ventilation hole (diameter 10 mm; covered by fine-mesh metal screening) centered at the top, and with four cork holes (diameter of each, 10 mm) spaced evenly around the top of each cage, each hole was 10 mm from the edge of the cage top. The cages rested on plas-

tic pots filled with water. A cotton roll (diameter 5 mm, length 40 mm) was inserted through a hole centered in the bottom of each cage. By protruding from the bottom of the cage into the pot of water, the cotton roll remained water logged for the duration of each test and provided humidity and drinking water for the spiders and the ants inside the cage. Four green mango leaves (each c. 150 mm long), each still attached to a stem (one leaf per stem, stem c. 200 mm long), were wedged into each cage. Numerous trials were run simultaneously.

A large number of major workers were collected from a single representative colony of *O. smaragdina* in a mango tree. These ants were then maintained as a 'laboratory colony' in a large terrarium. From this large laboratory colony, we established smaller groups in the cages by placing a specified number (10, 20, 40) of workers in each cage 16 h before testing began. Whenever the laboratory colony was depleted, we replenished it by collecting

more major workers from the same field colony as before.

Testing began by introducing a single salticid through one of the cork holes at the top of the cage, with a rule that no ants could be within 50 mm of the hole when the salticid was introduced. With four cork holes to choose from, this criterion was always achievable. Each test spider was first taken into a 40 mm long (diameter 5 mm) clear glass tube (plugged by a cork at both ends). After 10 min the corks from the tube and a hole in the top of the cage were removed and the open end of the tube was placed against the open hole of the cage. If the spider did not enter the cage immediately, the cork at the other end of the tube was removed and a brush was used gently to push the spider out of the tube and into the cage. For each combination of salticid species and each ant-group size, equal numbers of tests ($n = 100$) were carried out. Between tests, cages were wiped clean with 80% ethanol, followed by distilled water. Transfer tubes and corks were also cleaned with 80% ethanol, followed by distilled water. The cleaning routine was a precaution against the possibility that chemical traces from previous ants and salticids might influence test outcomes.

RESULTS

Data from testing with each ant-group size are considered separately. However, within each group size, we pooled many of the data sets that were not significantly different from each other (in each instance, $P > 0.1$). For each species of salticid data for adults were pooled with data for juveniles. Data for the various species within each category were also pooled, resulting in three sets of pooled data (myrmecophagic, myrmecomorphic and ordinary). Data for myrmecophagic, myrmecomorphic and myrmecophilic salticids were then pooled and compared with *Myrmarachne assimilis* and with ordinary salticids, greatly simplifying data presentation. However, the trends from using myrmecophagic, myrmecomorphic and myrmecophilic salticids also held, and were statistically significant, when myrmecophagic and myrmecomorphic salticids were each compared alone with *M. assimilis* and with ordinary salticids.

With each of the three ant-group sizes, the % survival of ordinary salticids was signifi-

cantly less than that of myrmecophagic, myrmecomorphic and myrmecophilic salticids (pooled) ($X^2 = 974.57$, $P < 0.001$, 10 ant tests) ($X^2 = 855.89$, $P < 0.001$, 20 ant tests) ($X^2 = 80.95$, $P < 0.001$, 40 ant tests) (Fig. 1). With groups of 40 ants, the % survival of *M. assimilis* was not significantly different from that of myrmecophagic, myrmecomorphic and myrmecophilic salticids (pooled) ($X^2 = 3.17$, $P = 0.075$). However, with smaller ant groups (20 or 10), the survival rate of *M. assimilis* was significantly higher than that of myrmecophagic, myrmecomorphic and myrmecophilic salticids (pooled) ($X^2 = 19.49$, $P < 0.001$, 10 ant tests) ($X^2 = 23.84$, $P < 0.001$, 20 ant tests).

DISCUSSION

The vicinity of weaver-ant colonies appears to be particularly dangerous for salticids, including salticids that mimic ants (i.e., ants are 'enemies'). In groups of 40 ants, few salticids survived, regardless of category. In groups of 10 and 20 ants, salticid survival fell into three clusters. Ordinary salticids had the lowest proportion of survivors and *M. assimilis* had the highest. Myrmecomorphic salticids (other than *M. assimilis*), myrmecophagic salticids and the myrmecophilic species (*Phintella piatensis*) had intermediate survival values.

That ordinary salticids had the lowest percentage of survivors was consistent with the earlier study (Nelson et al. 2004), but there were also some differences between the findings in this study and the earlier study. In the earlier study, ant mimics, ant eaters and *P. piatensis* (the myrmecophile) had distinguishably different survival values, but these categories were not discernible in the present study where we used groups of 10–40 ants. Another difference was that, in the earlier study, the proportion of surviving *M. assimilis* did not differ significantly from that of other ant mimics with a variety of ant species, whereas *M. assimilis* was clearly distinguishable from other ant mimics in the present study using only *O. smaragdina*.

For any salticid, avoidance might be the most straightforward protection from attacks by ants. Although spider eyes generally lack the structural complexity required for acute vision (Land 1985), salticids have unique, complex eyes (Land 1969a,b; Blest et al. 1990) that support resolution abilities with no

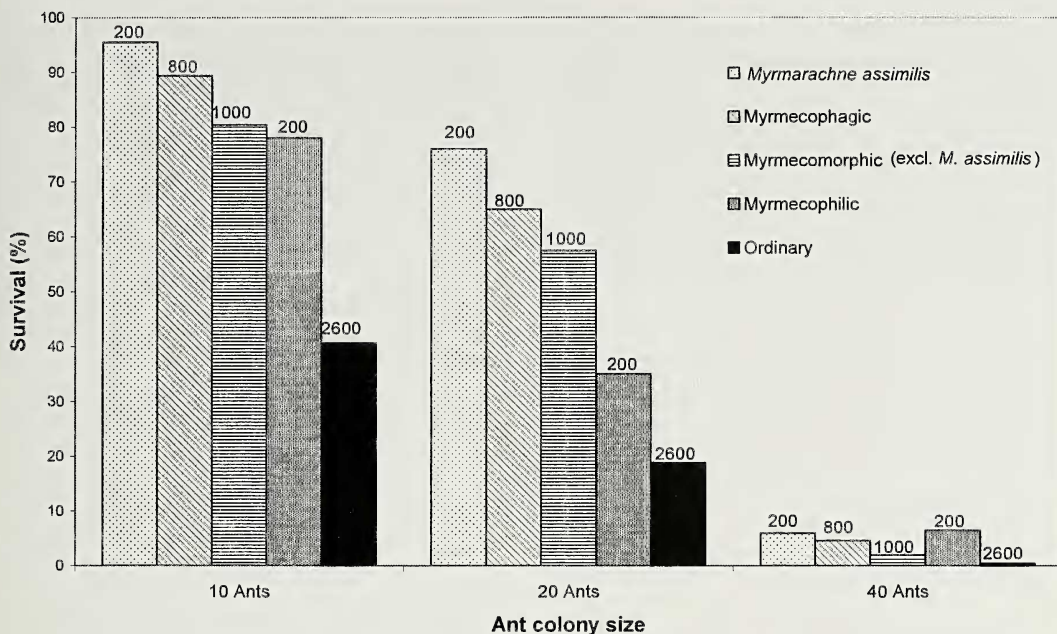


Figure 1.—Percent survival of different categories of salticids in tests with groups of *Oecophylla smaragdina* (Table 1). For each salticid species, with each ant-group size, $n = 200$ (100 adults and 100 juveniles). Data pooled in histograms. n for pooled data is indicated above each bar.

known parallels in other animals of comparable size (Land & Fernald 1992; Land & Nilsson 2002). Exceptional eyesight may enable salticids to be especially effective at detecting ants from a distance and avoiding dangerous proximity, but the strategies of myrmecophilic, myrmecomorphic and myrmecophagic salticids cannot be simply to avoid ants. For example, myrmecophagic salticids must at least intermittently come close enough to attack individual ants.

For *Myrmarachne*, the resemblance to the ant model appears to function primarily as Batesian mimicry. *Myrmarachne*'s mimicry of an aggressive model puts these salticids in a difficult situation. Successfully using mimicry to achieve safety from other predators would seem to require that individuals of *Myrmarachne* come close to the ants that serve as their models, but they must, at the same time, avoid becoming the model's prey (see Reiskind 1970; Edmunds 1974; Elgar 1993; Oliveira 1988). For *M. assimilis*, the problem is specifically how to stay close enough to be an effective Batesian mimic of one of its own especially dangerous predators, *O. smaragdina* (Nelson et al. 2004).

Our hypothesis was that *M. assimilis* has

evolved adaptations that make it especially proficient at surviving in the presence of its model and our findings support this hypothesis. However, further research is needed for clarifying precisely what these adaptations might be. Ants rely primarily on chemical, not visual, information for detecting other ants (Hölldobler & Wilson 1990). Many ants use cuticular hydrocarbons to distinguish between nestmates and non-nestmates (Hölldobler & Wilson 1990; Thomas et al. 1999; Wagner et al. 2000). The salticid spider *Cosmophasis bi-taeniata* (Keyserling 1882) associates with *O. smaragdina* and is an exploitative chemical mimic of its host (Allan & Elgar 2001; Allan et al. 2002). Whether *M. assimilis* uses a similar strategy to avoid predation by *O. smaragdina* while in the vicinity of its model has not been investigated. However, in this study, the salticids were from laboratory cultures and, unless it was during the duration of the tests itself, they could not have acquired any host-specific cuticular hydrocarbons from ants by direct contact with, or close proximity to, the ants.

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